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Old-growth forests as global carbon sinks

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Old-growth forests remove carbon dioxide from the atmosphere^{1,2} at rates that vary with climate and nitrogen deposition³. The sequestered carbon dioxide is stored in live woody tissues and slowly decomposing organic matter in litter and soil⁴. Old-growth forests therefore serve as a global carbon dioxide sink, but they are not protected by international treaties, because it is generally thought that ageing forests cease to accumulate carbon^{5,6}. Here we report a search of literature and databases for forest carbon-flux estimates. We find that in forests between 15 and 800 years of age, net ecosystem productivity (the net carbon balance of the forest including soils) is usually positive. Our results demonstrate that old-growth forests can continue to accumulate carbon, contrary to the long-standing view that they are carbon neutral. Over 30 per cent of the global forest area is unmanaged primary forest, and this area contains the remaining old-growth forests⁷. Half of the primary forests (6×10^8 hectares) are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, these forests alone sequester about 1.3 ± 0.5 gigatonnes of carbon per year. Thus, our findings suggest that 15 per cent of the global forest area, which is currently not considered when offsetting increasing atmospheric carbon dioxide concentrations, provides at least 10 per cent of the global net ecosystem productivity⁸. Old-growth forests accumulate carbon for centuries and contain large quantities of it. We expect, however, that much of this carbon, even soil carbon⁹, will move back to the atmosphere if these forests are disturbed.

We conducted a literature search to test the hypothesis that old-growth forests continue to accumulate atmospheric carbon dioxide (CO₂). Site-level estimates of the annual sums of carbon-cycle components were compiled, including those of biometry-based net primary production (NPP), eddy-covariance or biometry-based net ecosystem production (NEP) and chamber-based heterotrophic respiration. The data set was completed with site information related to stand characteristics, standing biomass and stand age. Data were compiled from 519 plot studies that reported one or more components of the carbon cycle. The studies involved boreal (~30%) and temperate (~70%) forests and represented the full range of conditions of such forests, excluding those subjected to experimental treatments such as fertilization and irrigation (Supplementary Information, section 1.1). Tropical forests were excluded from the analysis because only 12 sites were found for which NEP and age estimates are available.

The NEP is the net carbon balance of the forest as a whole, and is the difference between CO₂ uptake by assimilation and losses through plant and soil respiration. On the basis of our global data set we find that in forests between 15 and 800 years old, the NEP is usually positive; that is, the forests are CO₂ sinks (Fig.1a). The maximum probabilities of finding a single forest to be a source of carbon at 60, 180 and 300 years of age are 0.20, 0.25 and 0.35, respectively. However, the probability of finding an ensemble of ten old-growth forests that are carbon neutral is negligible (Supplementary Fig.1). In the small number of case studies on the effect of age on the carbon balance of forests, several have demonstrated some age-related decline in NEP but very few have shown old forests to be sources^{1,2,10-13}. Our NEP estimates suggest that forests 200 years old and above sequester on average 2.4 ± 0.8 tC ha⁻¹ yr⁻¹ (tC, tonnes of carbon; Fig.1a). In our model (Supplementary Information, section 1.3), we find that old-growth forests accumulate 0.4 ± 0.1 tC ha⁻¹ yr⁻¹ in their stem biomass and 0.7 ± 0.2 tC ha⁻¹ yr⁻¹ in coarse woody debris, which implies that about 1.3 ± 0.8 tC ha⁻¹ yr⁻¹ of the sequestered carbon is contained in roots and soil organic matter. The commonly accepted and long-standing view that old-growth forests are carbon neutral (that is, that photosynthesis is balanced by respiration) was advanced in ref. 6 and was originally based on ten years' worth of data from a single site⁵. It is supported by the observed decline of stand-level NPP with age in plantations^{14,15}, but is not apparent in some ecoregions¹⁶. Yet a decline in NPP is commonly assumed in ecosystem models (Supplementary Information, section 1.4). Moreover, it has led to the view that old-growth forests are redundant in the global carbon cycle.

If, however, the hypothesis of carbon neutrality⁶ were correct, the expected probabilities of observing a sink or source would be equal and around one-half, the average sink strength for a random ensemble of forests 200 years old and above would be zero and the mean CO₂ release from heterotrophic respiration would equal the mean CO₂ sequestration through NPP (thus, the ratio of heterotrophic respiration to NPP would be approximately one). However, we observe this ratio to be well below one on average (Fig. 1b) and not to increase with age. Hence, all three quantitative tests fail to support the hypothesis of carbon neutrality. The currently available data consistently indicate that carbon accumulation continues in forests that are centuries old.

In fact, young forests rather than old-growth forests are very often conspicuous sources of CO₂ (Fig. 1a) because the creation of new forests (whether naturally or by humans) frequently follows disturbance to soil and the previous vegetation, resulting in a decomposition rate of coarse woody debris, litter and soil organic matter (measured as heterotrophic respiration) that exceeds the NPP of the regrowth^{2,17-22} (Fig.1b). The scatter in the relationship between NPP and age is considerable, but given the climatic, edaphic and biological diversity of the observations in combination with differences in disturbance histories, this is to be expected. There is some degree of age-related decline in NPP beyond 80 years of age (Fig.1c), and temperate and boreal forests both show a consistent pattern of declining NPP beyond an early maximum (Supplementary Fig.2a) when analysed separately. The decline in NPP could be partly attributed to the presence or absence of management (Supplementary Fig.2b). However, we expect that this decline is not strictly a management effect, but a reflection of differences in disturbance history between managed and unmanaged forests.

Consistent with earlier studies², biomass continues to increase for centuries irrespective of whether forests are boreal or temperate (Supplementary Fig.3). In the course of succession, plants compete for resources and self-thinning²³ (or thinning by humans in the case of managed forests) occurs (Fig.2), so the older stands contain a relatively small number of individuals, although of course these trees tend to be large. Obviously biomass cannot accumulate forever. Our data (Supplementary Fig.3) suggest a possible upper limit some-where between 500 and 700 tC ha⁻¹ (equivalent to 1,400 to 1,800 cubic metres of wood per hectare); these high-biomass forests were located in the Pacific Northwest USA¹⁶.

We speculate that when high above-ground biomass is reached, individual trees are lost because of lightning, insects, fungal attacks of the heartwood by wood-decomposers, or trees becoming unstable in strong wind because the roots can no longer anchor them. If old-growth forests reach high above-ground biomass and lose individuals owing to competition or small-scale disturbances, there is generally new recruitment or an abundant second canopy layer waiting in the shade of the upper canopy to take over and maintain productivity.

Although tree mortality is a relatively rapid event (instantaneous to several years long), decomposition of tree stems can take decades. Therefore, the CO₂ release from the decomposition of dead wood adds to the atmospheric carbon pool over decades, whereas natural regeneration or in-growth occurs on a much shorter timescale. Thus, old-growth forest stands with tree losses do not necessarily become carbon sources, as has been observed in even-aged plantations (that is, where trees are all of the same age). We recognize that self-thinning theory was originally developed and validated for even-aged single-species stands; however, it has been shown to hold for uneven-aged multi-species plant communities (Supplementary Information, section 1.3). In reasonable agreement with our observations (Fig.1b), self-thinning theory predicts that the ratio between heterotrophic respiration and NPP is constant and around 0.65 ± 0.02 (indicating a carbon sink; Supplementary Fig.4), as long as stand density is driven by small-scale, rather than stand-replacing, disturbances. Old stands, with sufficiently high densities (that is, through development of a multilayer canopy structure) are thus expected to maintain biomass accumulation for centuries. Hence, we postulate that bio-mass accumulation and decline are largely driven by stand structure.

A stand must be spared for centuries from stand-replacing disturbances (such as fires, insect outbreaks, wind-throw and avalanches) in order to accumulate sufficient aboveground biomass to become old growth. Because the cumulative probability of disturbances is higher in stands with high above-ground biomass, old stands are rarer than young stands, even in unmanaged landscapes. At the land-scape level, we expect a mosaic of forests characterized by different times since the last stand-replacing disturbance²⁴. Despite differences in age and density, these forests are, however, expected to follow the same relationship between biomass and density (Fig.2).

Figure 1 — Changes in carbon fluxes as a function of age. a, Observed NEP versus age; positive values indicate carbon sinks and negative values indicate carbon sources. b, Observed ratio of heterotrophic respiration (Rh) to NPP versus age; $Rh:NPP < 1$ indicates a carbon sink. c, Observed NPP versus age. It appears that temperate and boreal forests both show a pattern of declining NPP. Most probably, the late-successional increase in NPP is caused by the combination of data from different climate regions or the combination of disturbance regimes (Supplementary Fig. 2a, b). In each panel, the green dots show observations of temperate forests, the orange dots show observations of boreal forests, the thick black line shows the weighted mean within a moving window of 15 observations, the grey area around this line shows the 95% confidence interval of the weighted mean and the thin black lines delineate the 95% confidence interval (where visible) of the individual flux observations.

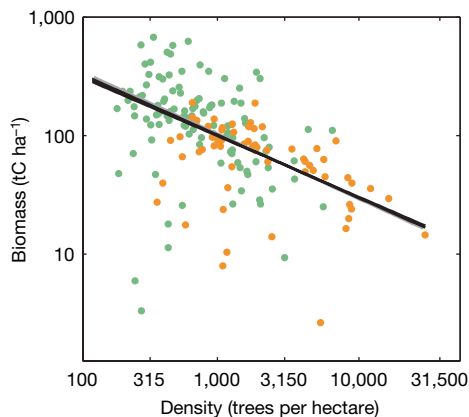
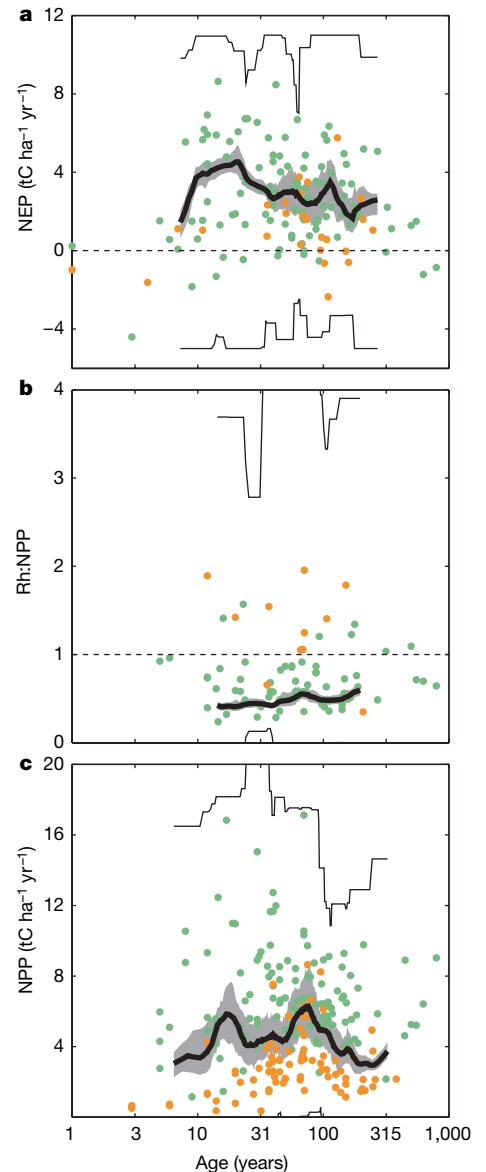


Figure 2 — Biomass accumulation as a function of stand density. Each data point represents a different forest, many of which have different growing conditions and tree species. Not all growing conditions and species compositions allow for the accumulation of the global maximum observed biomass. Self-thinning, the process of density-dependent mortality, is shown (solid line, of slope c) as the relationship between the logarithm of above-ground biomass and the logarithm of stand density according to ref. 23 ($\gamma = -0.51 \pm 0.08$, $r^2 = 0.25$, $P < 0.01$). The green dots show observations of temperate forests, the orange dots show observations of boreal forests and the grey area (which is barely wider than the solid line) shows the 95% confidence interval of the median.



Under the Kyoto Protocol (<http://unfccc.int/resource/docs/convkp/kpeng.pdf>) only anthropogenic effects on ecosystems are considered (Article 2 of the Framework Convention on Climate Change (<http://unfccc.int/resource/docs/convkp/conveng.pdf>); Supplementary Fig.5) and the accounting for changes in carbon stock by afforestation, reforestation and deforestations is mandatory (Article 3.3), operating from a base line of 1990. Leaving forests intact was not perceived as an anthropogenic activity. In addition, the potential consequences of excluding old-growth forests from national carbon budgets and from the Kyoto Protocol were downplayed in the carbon-neutrality hypothesis⁶. However, over 30% (1.3×10^9 ha) of the global forest area is classified⁷ by the Food and Agriculture Organization of the United Nations as primary forest, and this area contains the world's remaining old-growth forests. Half (0.6×10^9 ha) of the primary forests are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, we expect that these forests alone sequester at least 1.3 ± 0.5 GtC yr⁻¹. Hence, 15% of the global forest surface, which is currently not being considered for offsetting increasing atmospheric CO₂ concentrations, is responsible for at least 10% of the global NEP⁸. Sporadic disturbances will interrupt carbon accumulation, implying that net biome productivity²⁵ will be lower, but it will remain positive as demonstrated by the accumulation of carbon in soils^{4,26}, coarsewoody debris and charcoal^{27,28}. The present paper shows that old-growth forests are usually carbon sinks. Because old-growth forests steadily accumulate carbon for centuries, they contain vast quantities of it. They will lose much of this carbon to the atmosphere if they are disturbed, so carbon-accounting rules for forests should give credit for leaving old-growth forest intact.

METHODS SUMMARY

We conducted a literature and database search to determine the fate of the carbon sequestered in forests. Observation-based estimates were compiled for carbon-cycle components, including biometry-based NPP, eddy-covariance or biometry-based NEP and chamber-based heterotrophic respiration²⁹. The data set was extended with site information related to stand characteristics, standing biomass and stand age. In general, uncertainties in flux estimates were not reported in the literature. Therefore, we estimated the total uncertainty for every component flux contained in the data set using a consistent framework based on expert judgment (Supplementary Information, section 1.2). The uncertainty framework in our data-base was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (that is, gap filling and dark respiration). Also, an uncertainty of 20% was assigned to the biomass, age and density estimates. These uncertainties were propagated through the statistical analyses by means of random realizations based on Monte Carlo principles. Within each of the 1,000 random realizations, normally distributed random errors, based on the uncertainty framework of our database, were added to the observed fluxes. Therefore, all results that are based on flux data are reported as the weighted mean and the 95% confidence interval of the probability distribution. Despite the climatic, edaphic and biological diversity of our observations, above-ground biomass was observed to be related to stand density in the way described by self-thinning theory²³. Although, this theory was initially developed for even-aged single-species plant communities, we applied it to our data (Supplementary Information, section 1.3) to determine the components of the flux-computed NEP, specifically the above-ground biomass, woody debris and soil sequestration. Furthermore, self-thinning theory was used to calculate the theoretical ratio of heterotrophic respiration to NPP and compare it with the observed ratio in support of the hypothesis that biomass accumulation and decline are largely driven by stand structure.

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Author Contributions S.L., B.E.L., A.K. and P.C. compiled the data set. S.L., A.B. and D.H. wrote code and analysed the data. S.L., E.-D.S., A.K., B.E.L., P.C. and J.G. designed the analyses and wrote the manuscript.

1 Methods and materials

1.1 Data selection for this study

We compiled a comprehensive database (see §1.2) on carbon fluxes, ecosystem properties and stand characteristics of forest stands²⁹. For this study, the database was queried for biometric-based NPP, chamber-based Rh, eddy-covariance or biometric-based NEP, their uncertainties and ecosystem attributes such as aboveground biomass, stand age, stand height and stand density. The quality of the data set used in this study was enhanced by excluding model-based flux estimates and flux estimates for fertilized and irrigated experimental treatments. Data from a total of 519 temperate and boreal forests that reported one or more of the variables were used in this study.

1.2 The database

A comprehensive relational database structure was designed to store information on carbon fluxes, ecosystem properties, and site information of forest stands. Data entries originated from peer-reviewed literature, established databases e.g.^{30,31} and personal communications with research groups involved in regional networks (AmeriFlux, AsiaFlux, CarboEurope-IP, ChinaFlux, Fluxnet-Canada, NECC, TCOS-Siberia, USCCC), and the Fluxnet project³². The high quality of the database is ensured by several features: (i) referential integrity is ensured by the structure of the database, (ii) literature and databases are browsed without discrimination for sites, regions, biomes or climate zones; data selection is only based on strict methodological criteria, (ii) consistency of the NPP data is ensured by a hierarchical framework, (iv) uncertainty of the fluxes are

estimated in a consistent manner accounting for the methodological approach and the length of the time series, (v) the uncertainty of aggregated fluxes is estimated, and (vi) a variety of observed and/or modelled meta-data is included in the database.

Structure of the database

The database is structured by site. A site is a forest or a stand with a known geographical location, biome (USA Department of Agriculture biome classification³³), tree species composition and management regime. Hence, different treatments within an experimental forest or different aged stands that form a chronosequence were recorded as different sites. Each site in the database is linked to at least one carbon balance component and each component is further linked to the methodology that was used to estimate it. Due to its structure, the database can contain multiple estimates of the same flux for the same year (i.e. if these estimates were reported in different studies or estimated with different measurement techniques). Because data from different sources or references are stored as different entries, the structure of the database thus ensures referential integrity.

Selection criteria

NPP estimates were included in the database when they were based on direct measurements of the main components of NPP³⁴ if these achieved these criteria: the net annual production of leaves or needles was determined by collecting leaf/needle fall throughout the year; annual stem and branch increment were determined using species- and region-specific allometric equations relating aboveground woody biomass increment to the change in basal area of individual trees in the plot; and coarse-root production was

determined through species- and region-specific allometric equations relating root mass to basal area and fine-root production was determined by repeated soil coring, isotopic estimates of fine-root turnover combined with biomass measurements, upscaled root-length production observed in minirhizotrons or the soil respiration and litterfall constraint formulated by Raich and Nadelhoffer (1989)³⁵. Furthermore, to be included in the database, foliage, stem, branch, coarse and fine root biomass increment had to be corrected for the annual litterfall of these components.

Direct measurements of annual and multiple-year NEP were included in the database when based on continuous measurements with a tower-based eddy covariance system. NEP estimates were accepted when data gaps due to system failure, stable atmospheric conditions or data rejection were filled by means of standardized methods^{36,37} to provide complete datasets. These data, however, do not include corrections for possible effects of advection, which may lead to a biased night time respiration even at high turbulence.

Biometric NEP estimates were included in our database when they were based on the difference between biomass production and heterotrophic respiration e.g. see³⁸ or repeated biomass inventories and soil respiration measurements e.g. see³⁹.

Estimates of heterotrophic respiration R_h were included in the database when based on subtracting chamber measurements from undisturbed plots from measured and up-scaled root respiration⁴⁰ or chamber measurements after trenching or girdling.

Consistency of the flux data

Although NPP data are more widely available than other carbon-flux estimates, there are considerable problems of consistency among NPP studies. Reported NPP values can range from the net primary production of a single component (e.g. foliage NPP) to the complete NPP of the ecosystem. In this study we accounted for these inconsistencies by combining 6 components and 4 aggregation levels of NPP in a hierarchical framework. For more details see Fig. 1 in²⁹. At the lowest hierarchical level, stem and foliage NPP were used to calculate aboveground NPP (ANPP₁; foliage + stem NPP). The next hierarchical level included branch NPP. If branch NPP was measured, wood NPP (stem + branch NPP) and ANPP₂ (foliage + stem + branch NPP or foliage + wood NPP) were calculated. Coarse and fine root NPP were recorded as separate components and summed to obtain the below ground NPP (BNPP₁; coarse + fine roots NPP). If all required low level components were available, the total NPP (TNPP₁) was calculated as ANPP₂ + BNPP₁. The framework was considered hierarchical because a certain level of NPP was calculated only when all underlying components were measured.

Given this careful processing and quality evaluation of data for each site, the NPP data are consistent when a single level of NPP data is used. It should be noted that minor inconsistencies remain within an individual component (i.e. the use of different cut-off diameters between coarse and fine roots). However, the variation due to these inconsistencies is expected to disappear when NPP estimates of a higher level are used (i.e. the variation due to different cut-off diameters are expected to disappear when total belowground NPP (BNPP₁) is used).

Uncertainty of the measured CO₂-fluxes

Our flux data span multiple biomes and the data come from diverse sources. Different biomes have different sources of uncertainty^{41,42}. Although recently efforts have been made to quantify the uncertainties of eddy covariance measurements⁴³⁻⁴⁷, uncertainty of CO₂-flux estimates are only rarely reported in the literature and when reported it is often unclear whether the given value denotes instrumental, spatial, temporal and/or other sources of variability. Therefore, we did not use the reported uncertainty and instead estimated the total uncertainty for every component flux contained in the database. The uncertainty was estimated in a uniform way based on expert judgment⁴⁸. We could not identify prior information that could constrain the absolute range of the estimated NEP. Without measurements or prior information, experts agreed that the NEP of a forest most likely ranges from -100 to 600 g C m⁻² yr⁻¹. The absolute range of the NEP estimate is thus ± 350 g C m⁻² yr⁻¹ (²⁹). However, all methodological approaches contained in the database used site-specific observations and are therefore expected to reduce the uncertainty surrounding the NEP estimates. Hence, the uncertainty was reduced with a method-specific factor. When NEP was determined by eddy covariance measurements the method-specific factor was set to 0.3 or 30% of 350 g C m⁻² yr⁻¹ to reproduce the uncertainty estimate of 105 g C m⁻² yr⁻¹ presented by⁴⁹⁻⁵¹. The other method-specific reduction factors were then set between 0.2 and 1.0 and selected by expert judgment. The applied method-specific reduction factors (i.e. 30% for eddy covariance), are tabulated in²⁹. When a flux was a multiple-year mean value, its value is less prone to inter-annual

variability and therefore its uncertainty (s_{ij}) was further reduced by accounting for the length of the time series. Thus:

$$s_{ijl} = (p_i \times RF_j) / \sqrt{l_{ijl}} \quad (1)$$

Where p_i is the initial uncertainty for site i in the absence of measurements (see Table 2 in²⁹) and RF_j is the reduction factor for method j according to Luysaert et al.²⁹ and l_{ij} is the length of the time series (in years) for site i for which the fluxes were estimated with method j in year l . Our uncertainty framework resulted in 95% confidence intervals (based on s_{ijl}) ranging between 105 and 350 g C m⁻² yr⁻¹ for NEP.

A similar approach was followed to estimate the uncertainty of NPP and Rh. However, for these fluxes the latitude of the site contained prior information regarding their absolute range (i.e. NPP at a boreal site is likely lower than the NPP at a temperate site²⁹). Consequently, the absolute range for NPP in the absence of measurements depends on the latitude. For each site contained in the database the latitude was known and as such, the absolute range in the absence of measurements (p_i) could be estimated. This initial uncertainty was then reduced by the method-specific factor and further adjusted for the length of the time series. Our uncertainty framework resulted in 95% confidence intervals ranging between 110 and 545 g C m⁻² yr⁻¹ for NPP. This range compares to uncertainties reported for a single forest^{34,52}. The 95% confidence intervals of Rh ranged between 95 and 295 g C m⁻² yr⁻¹. We are not aware of observation-based studies that report the uncertainty of Rh observations. Therefore, the spatial variability of Rh in the database (250 g C m⁻² yr⁻¹) was used to validate the expert-based assessment.

Aggregated fluxes and their uncertainty

According to the analyses presented in this study the data had first to be aggregated by year and then by site. For a given site (i), a single weighted mean flux estimate (F) was produced for each available year l . When the flux component was determined with k different methods j in year l , the flux determined by method j for site i was then given as F_{ijl} . The average flux across methods (F_{il}) was calculated as the weighted mean:

$$F_{il} = \sum_{j=1}^k \left(w_{ijl} \times F_{ijl} / \sum_{j=1}^k w_{ijl} \right) \quad (2)$$

Where, $w_{ijl} = 1 / s_{ijl}^2$. The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_{il} = \sqrt{\sum_{j=1}^k s_{ijl}^4 \times w_{ijl}} \quad (3)$$

Following, the weighted mean flux component was calculated across years:

$$F_i = \sum_{l=1}^m \left(w_{il} \times F_{il} / \sum_{l=1}^m w_{il} \right) \quad (4)$$

Where, $w_{il} = 1 / s_{il}^2$, m the number of years for which flux estimates are available for site i .

The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_i = \sqrt{\sum_{l=1}^m s_{il}^4 \times w_{il}} \quad (5)$$

Site description data

Additional site information related to stand characteristics, standing biomass, leaf area index and growing environment were added to the database as separate tables. Stand characteristics such as basal area, mean tree diameter, mean tree height, mean tree density and mean stand age are available for many sites. Also the observed standing biomass and its major components, the maximal observed leaf area index, and some methodological details of the leaf area measurement technique were available and stored in the database for many sites.

Availability of the database

The database its manual and appendices can be downloaded from ftp://ftp.bgc-jena.mpg.de/pub/outgoing/mjung/CfluxDB_Luyssaert/ and <http://www.ua.ac.be/main.aspx?c=sebastiaan.luyssaert&n=35884>

1.3 Self-thinning and data modeling

Self-thinning is the process of density-dependent mortality. For even-aged, single species stands Yoda *et al.*²³ proposed an empirical summary of this process:

$$W = c \cdot n^{\gamma-1} \quad (4)$$

where W is the mean biomass of an individual tree (g tree^{-1}), n the decreasing stand density (tree m^{-2}), and c a stand-specific constant ($\text{g m}^{2(\gamma-1)} \text{tree}^{-\gamma}$) that depends on species, light regime and nutrition status. The exponent γ (dimensionless) has been

derived from tree geometry (i.e. height and ground area)²³. The biomass per unit area (B ; g m^{-2}) equals the product of W and n , therefore, the self thinning law for stands is derived by multiplying Eq. 4 by n :

$$B = c \cdot n^\gamma \quad (5)$$

Taking the logarithm of this equation yields a linear relationship:

$$\log(B) = \log(c) - \gamma \cdot \log(n) \quad (6)$$

For even-aged single-species stands γ was estimated at -0.5 (²³) In Fig. 2 we used the functional relationship of Eq. 6 and estimated c and γ at the biome-level. During the life-time of a forest its density decreases from n_{start} to n_{end} , $n_{end} - n_{start}$ individual trees will be lost. The biomass of each tree is given by Eq. 4 and the total loss of biomass (L) during the life-time of the forest is given by:

$$L = \sum_{n_{start}}^{n_{end}} c \cdot n^{\gamma-1} \quad (7)$$

At the same time the standing biomass increased according to Eq. 5:

$$G = c \cdot (n_{end} - n_{start})^\gamma \quad (8)$$

Self-thinning theory was originally developed and validated for even-aged single-species stands. Since it was first published, it has been shown to be equally valid for uneven-aged multi-species plant communities^{53,54}. Applying Eqs. 4 to 8 to uneven-aged forests requires that the biomass of recruitment is negligible. In the old growth beech forest of Hainich¹¹ the upper canopy layer accounted for 91% of the biomass, the 2nd canopy for 9% and recruitment for less than 1%. Consequently, ignoring recruitment most likely will result in only small errors in G and L . There are no theoretical grounds for not being able to apply self-thinning estimates to multi-species plant communities because the primary driver of self-thinning is similarity in resource use⁵⁵; the trade-off between density and size will be compensated among species⁵⁶. Consistent with this, we observed that all boreal and temperate forests (Fig. 2), including the sub set of unmanaged boreal and temperate forests (not shown), followed the self-thinning theory with γ approaching -0.5. We interpreted this as a negligible effect of recruitment and species interactions on biomass and, therefore, used the observed relationship between biomass and density data to calculate a proxy for NPP and Rh components of flux-computed NEP. Nevertheless, these proxies were only used for interpretation of the primary results. Thus, all green and orange symbols (Figs 1, 2, S2, S3 and S4) are field-observations.

In this study, self-thinning theory was only applied to: (1) estimate the expected ratio between Rh and NPP across densities and (2) estimate the importance of woody biomass production in NEP of old forests. First, the gross biomass production (B_{gross}) (including branches, stem and coarse roots) is thus $G+L$. G , L and B_{gross} can be calculated for tree-by-tree changes in density from n_{start} to n_{end} (Fig. S5a). Following a change in density, the

sequestered carbon is then given by the difference of B_{gross} before and just after tree mortality occurred. The carbon released through decomposition of woody debris is given by L (Fig. S5b). Assuming foliage and fine root NPP and their decomposition offset each other, allows us to apply $\Delta L:\Delta B_{gross}$ as a proxy for Rh:NPP (Fig. S5c). It should, however, be noted that legacy woody debris that existed prior to stand establishment is not included in our estimate of L . With a decomposition rate of 1 to 3% yr^{-1} ⁵⁷, ΔL is likely to underestimate Rh for the first 30 to 100 years. Second, ΔB_{gross} (and ΔL) are expressed on a per tree basis (gC m^{-2} lost tree⁻¹) but need to be converted on a per year basis to obtain woody NPP ($\text{gC m}^{-2} \text{yr}^{-1}$). The observed maximum and minimum density for stands older than 200 years was used as n_{start} to n_{end} and the observed age range was used to determine the time required to realize this density decrease (lost tree yr^{-1}). ΔB_{gross} , Δn and Δt were combined to estimate woody NPP ($\text{gC m}^{-2} \text{yr}^{-1}$) for forests of 200 years and older.

1.4 Odum's hypothesis as an implicit assumption in ecosystem models

The mathematical equation which governs NEP in models is $dM/dt = NPP - k \cdot M$ where, M is the carbon stock (g C m^{-2}), k is a decay rate describing the biomass mortality and soil carbon decomposition and NPP ($\text{g C m}^{-2} \text{yr}^{-1}$) is the net primary production. When the modeled leaf area index (LAI), atmospheric CO_2 concentration and climate are constant, NPP is also constant. During a spin-up, which is required to reach steady state, LAI, atmospheric CO_2 concentration and climate are constant. Hence, M approaches NPP/k and thus dM/dt (or NEP) is zero. In addition, modeled forests are usually mature

but of unknown age. Consequently, in the absence of disturbances, ecosystem models predict that mature forests are carbon neutral and thus reflect Odum's hypothesis.

1.5 Data processing

The total uncertainty (s_i) for the flux contained in the data set were estimated using a framework based on expert judgment (See §1.2). The uncertainty framework was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (i.e. gap filling). The uncertainties were propagated throughout the analyses by means of random realizations based on Monte Carlo principles⁵⁸.

The 95% uncertainty interval for biomass, age and density was set to 20% of the observed values and the uncertainties for NPP, wNPP, Rh and NEP were extracted from the database. One thousand realizations of the dataset were simulated by adding a normally distributed uncertainty to the observed estimates for both the dependent and independent variable. The normally distributed uncertainties were calculated by multiplying the total uncertainty of the flux (s_i) by a normally distributed random number with a mean equal to zero and a variance equal to one. Following, each relationship or test between a dependent and independent variable was estimated a thousand times, once for each random realization.

For the relationships between age, NEP, Rh/NPP and NPP, the moving weighted mean was calculated for a moving window of 15 observations. For a given age we then plotted

the mean value for all 1000 simulations (i.e. black line) and the 95% confidence interval of the mean value (i.e. gray area around the black line). For a given age, the confidence interval was estimated as the 2.5 and 97.5 percentile of the mean values of the 1000 simulations. Also for a given age, the 2.5 and 97.5 percentile of all 1000 random realizations for the individual sites within a window of 15 observations was used as the uncertainty to estimate the probability that an individual forest is a source rather than a sink.

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Supplementary figures

Figure S1. Cumulative probability of finding a given mean NEP for a group of 10 randomly selected forests older than 200 years. The minimal group NEP for forests older than 100 years was $-0.5 \text{ tC ha}^{-1} \text{ yr}^{-1}$ with a probability of 0.0012 (negative value indicates a source), $-1.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$ for forests older than 200 years ($p = 0.0008$) and $-0.9 \text{ tC ha}^{-1} \text{ yr}^{-1}$ for forests older than 300 years ($p = 0.0007$). Overlapping cumulative distribution functions (not shown) suggested that the results did not depend on the selected age threshold when set to 100, 200 or 300 years. The group probabilities were calculated by simulating 1000 possible realizations of the NEP data and their uncertainties.

Figure S2. Changes in net primary production (NPP) as a function of forest age (a) Relationships of observed NPP vs. age where green shows the temperate and orange the boreal forests. The thick black line shows the weighted mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for temperate and boreal forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. It appears that temperate and boreal forests each show a pattern of declining NPP. Only when the two data sets are combined is the late-successional increase apparent. This reflects the lack of data from boreal forests older than 300 years, considering that boreal NPP is usually lower than temperate NPP. The apparent increase in NPP is likely because the available estimates for the oldest forests are dominated by data from temperate regions that have higher average NPP; (b) Relationship between observed NPP and age where green shows the unmanaged and brown the managed forests. The thick black line shows the weighted

mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for managed and unmanaged forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. NPP in unmanaged forests appears to be independent of age which could be due to differences in disturbance history.

Figure S3. Biomass accumulation as a function of stand age, shown as the relationship between aboveground biomass and the logarithm of stand age. The thick black line shows the weighted mean within a moving window of 15 observations. The grey area around this line shows the 95% confidence interval of the median. Each data point represents a forest stand (green is temperate, and orange is boreal), many of which have different growing conditions and species composition.

Figure S4. Productivity and productivity indexes derived from the self-thinning theory fitted to the observed biomass and density data. (a) Biomass losses (L ; blue line), net biomass stock (B , red line) and gross biomass stock (B_{gross} , green line) as a function of stand density. (b) Changes in gross biomass and biomass losses expressed per tree lost as a function of stand density. (c) $\Delta L:\Delta B_{gross}$ (dotted line and dark confidence intervals) as a proxy of $Rh:NPP$. $\Delta L:\Delta B_{gross}$ which was obtained from the self-thinning plot (Fig. 2) is in reasonable agreement with the observed $Rh:NPP$ (full line and light gray confidence intervals).

Figure S5. The reporting and accounting of carbon stocks under the UNFCCC is confined to national borders, because nations are the signing parties. Art. 2 of the UNFCCC calls for stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system⁵⁹. Art. 4.2(a) clarifies that this should be achieved by national policies and taking corresponding measures on the mitigation of climate change, by limiting its anthropogenic emissions of greenhouse gases and protecting and enhancing its greenhouse gas sinks and reservoirs. However, unmanaged systems (red area) are traditionally considered to be carbon-neutral and therefore only managed ecosystems are considered within the Framework (cyan area). Nations have to report their carbon-stocks according to the rules set by the IPCC Good Practice Guidance which includes land-use types of Cropland, Grassland, Forest, Wetlands and Settlements (light and dark cyan area). Under the Kyoto Protocol the accounting of changes in carbon-stock by afforestation, reforestation and deforestation (ARD) is mandatory (Art. 3.3). In addition, Nations can select to account for changes of carbon-stocks in cropland, grassland, forest and revegetation projects (dark cyan area) or exclude certain regions (i.e. USA-Alaska). Most European countries have selected to include only forestry into their accounting system and thus not account for carbon-stock changes in agriculture. In addition, flexible mechanisms allow trading of carbon credits between countries. Nations can also receive credits from land-use projects funded in other industrial countries via the Joint Implementation (JI) mechanism. So far, the land-use sector is excluded from the European carbon trade. Also, afforestation projects funded in non-annex I countries may be added to the national carbon-balance via the Clean Development Mechanism (CDM), but this amount will be negligible until 2012.

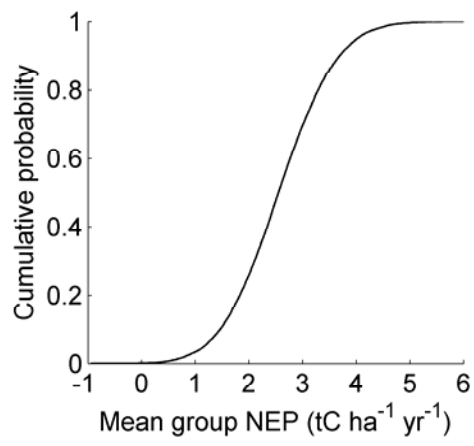


Figure S1

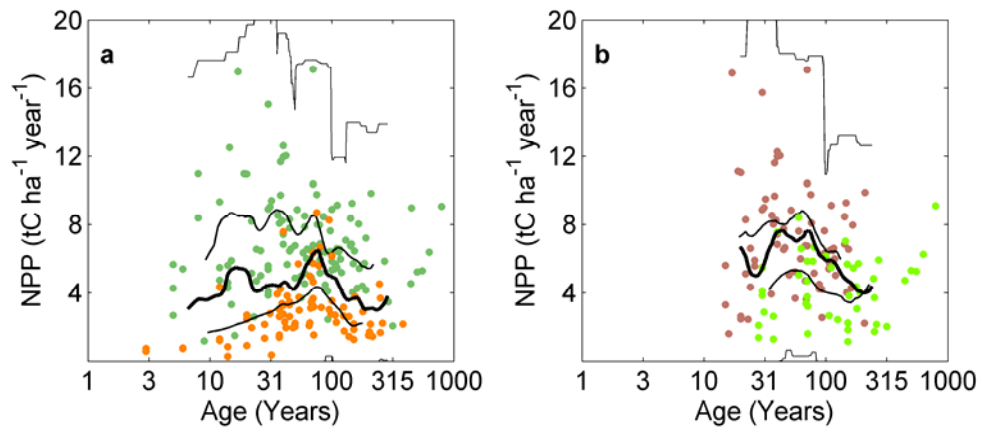


Figure S2

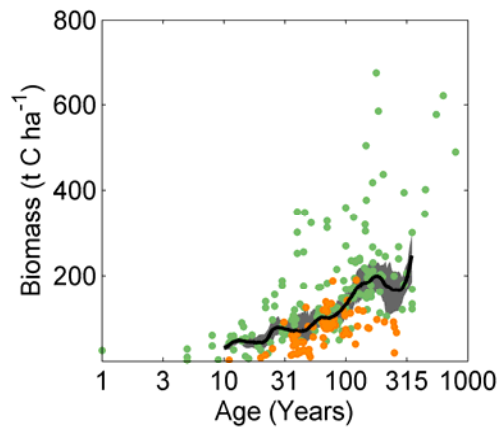


Figure S3

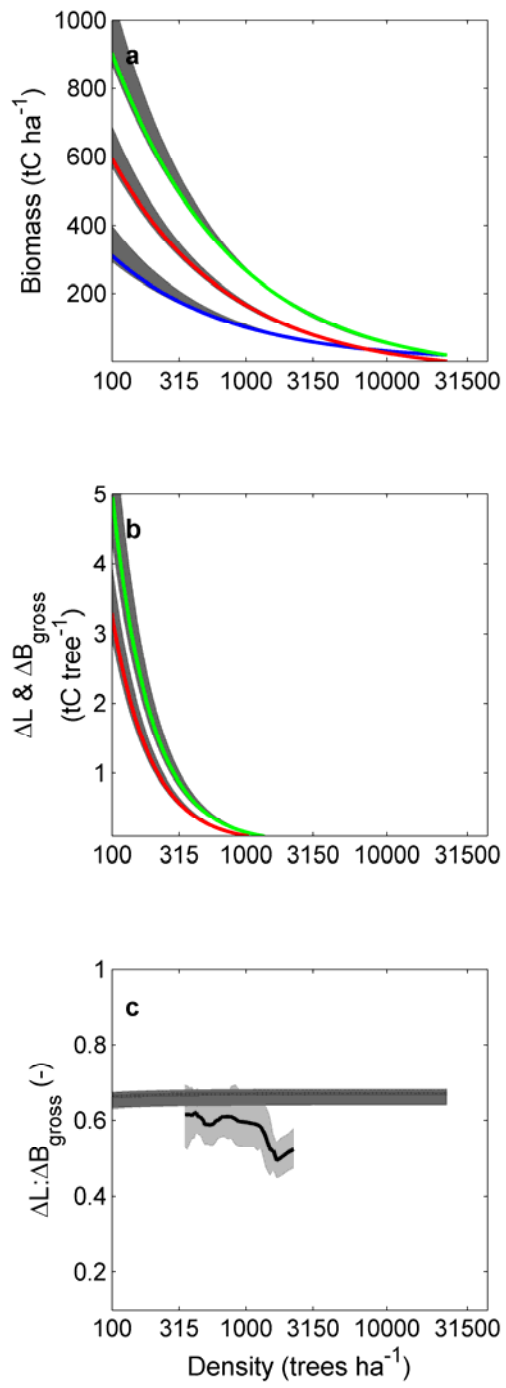


Figure S4

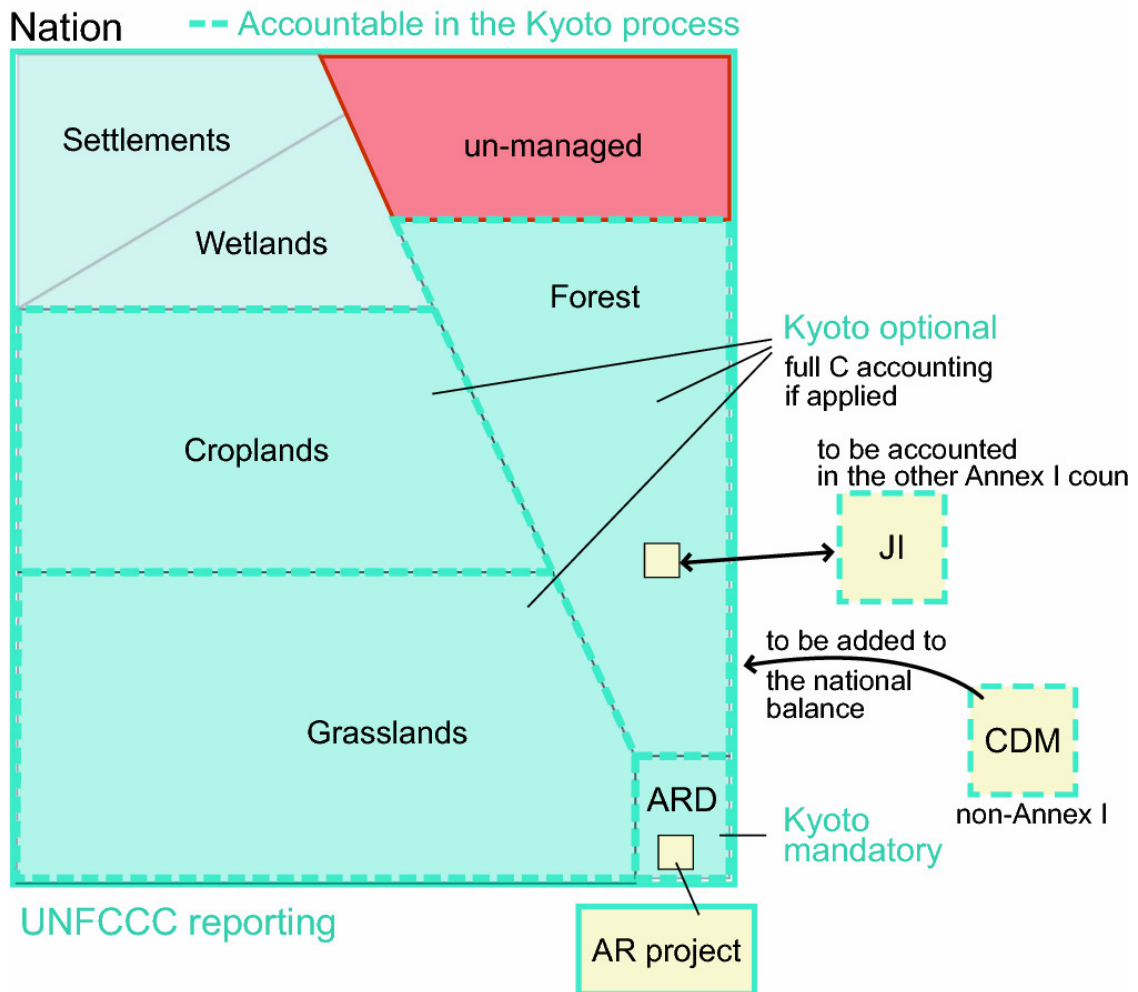


Figure S5